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Armillaria Root Rot in the Canadian Prairie Provinces

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NOTE

The exclusion of certain manufactured products does not necessarily imply disapproval nor does the mention of other products necessarily imply endorsement by Forestry Canada.

Root diseases are some of the most serious sources of disease loss in Canadian forests. These diseases affect all aspects of forest use. Trees that are used for fiber or lumber production as well as trees located in recreation sites are affected by these diseases. In 1976 damage from all diseases in Canadian forests was estimated to be 40.4 million m^3 of wood. Of this, root diseases were responsible for an annual loss of 5.1 million m^3 of wood: 1.7 million m^3/yr in mortality and 3.4 million m^3/yr in growth reduction (Canadian Forestry Service 1979). There are many wood decay fungi that can attack tree roots; however, laminated root rot, Annosus root rot, Armillaria root rot, and Tomentosus root rot are the leading causes of root disease in Canada. In the Canadian prairie provinces Armillaria root rot and Tomentosus root rot are the two major root diseases affecting trees.

Armillaria root rot is an important disease of both conifers and hardwoods throughout the world (Wargo and Shaw 1985; Kile et al. 1991). In Canada, Armillaria root rot occurs in all forested regions and is one of the most serious diseases of young conifers in the prairie provinces (Hiratsuka 1987). Armillaria root rot losses in the prairie provinces have been documented since 1951 (Riley et al. 1952). Until recently, relatively little was known about the disease in the prairie provinces. This report summarizes current knowledge of Armillaria root rot in the prairie provinces including the species of *Armillaria*, distribution, symptoms and signs of the disease, field detection and survey methods, damage, hosts, pathogenicity, epidemiology factors affecting the disease, and control measures.

Taxonomy of Armillaria Root Rot Pathogens

There are currently 36 described species of *Armillaria* in the world (Watling et al. 1991). Until recently Armillaria root rot was thought to be caused by the species *Armillaria mellea* (Vahl:Fries) Kummer, a species that was well known for the variability in its basidiocarp (mushroom) morphology. There has been considerable controversy over its ability to cause disease. In 1978, Ullrich and Anderson in the United States and Korhonen in Finland discovered that there were more than one species of *Armillaria* in North America and Europe capable of causing the disease. These species were recognized by being intersterile (incapable of breeding with one another). In North America they were termed North American biological species (NABS). Ullrich and Anderson (1978) and Anderson and Ullrich (1979) originally found ten of these NABS. Korhonen (1978) found five biological species in Europe that have been described by taxonomists (Roll-Hansen 1985). Anderson (1986) revised the original number of NABS from ten to eight; however, Morrison et al. (1985) discovered another, NABS XI, in British Columbia. Some of the NABS have been identified, based on basidiocarp characteristics, as described *Armillaria* species and others have been listed as new taxonomic species (Motta and Korhonen 1986; Bérubé and Dessureault 1988, 1989) (Table 1).

Currently three species of *Armillaria* have been collected in the prairie provinces: *A. ostoyae*, *A. sinapina* Bérubé & Dessureault, and *A. calvescens* Bérubé & Dessureault (Mallett 1990). Mallett (1989) found that *A. ostoyae* basidiocarps from the prairie provinces varied tremendously in size and morphology and noted that it was difficult to distinguish *A. ostoyae* from *A. sinapina* based strictly on basidiocarp morphology. Figure 1 shows several basidiocarps of both species. Identification of *Armillaria* species in the field is difficult; therefore, laboratory techniques using *Armillaria* isolates cultured from basidiocarps or diseased root material are necessary to provide accurate identifications.

Table 1. Identity of the North American Biological Species (NABS) of *Armillaria*

NABS	Species name
I	*Armillaria ostoyae* (Romagn.) Herink
II	*Armillaria gemina* Bérubé & Dessureault
III	*Armillaria calvescens* Bérubé & Dessureault
V	*Armillaria sinapina* Bérubé & Dessureault
VI	*Armillaria mellea* (Vahl.:Fries) Kummer
VII	*Armillaria gallica* Marxmüller & Romagn.
IX	taxonomically undescribed
X	taxonomically undescribed
XI	taxonomically undescribed

Note: Anderson (1986) has shown NABS IV and V to be interfertile and NABS VI and VIII to be interfertile.

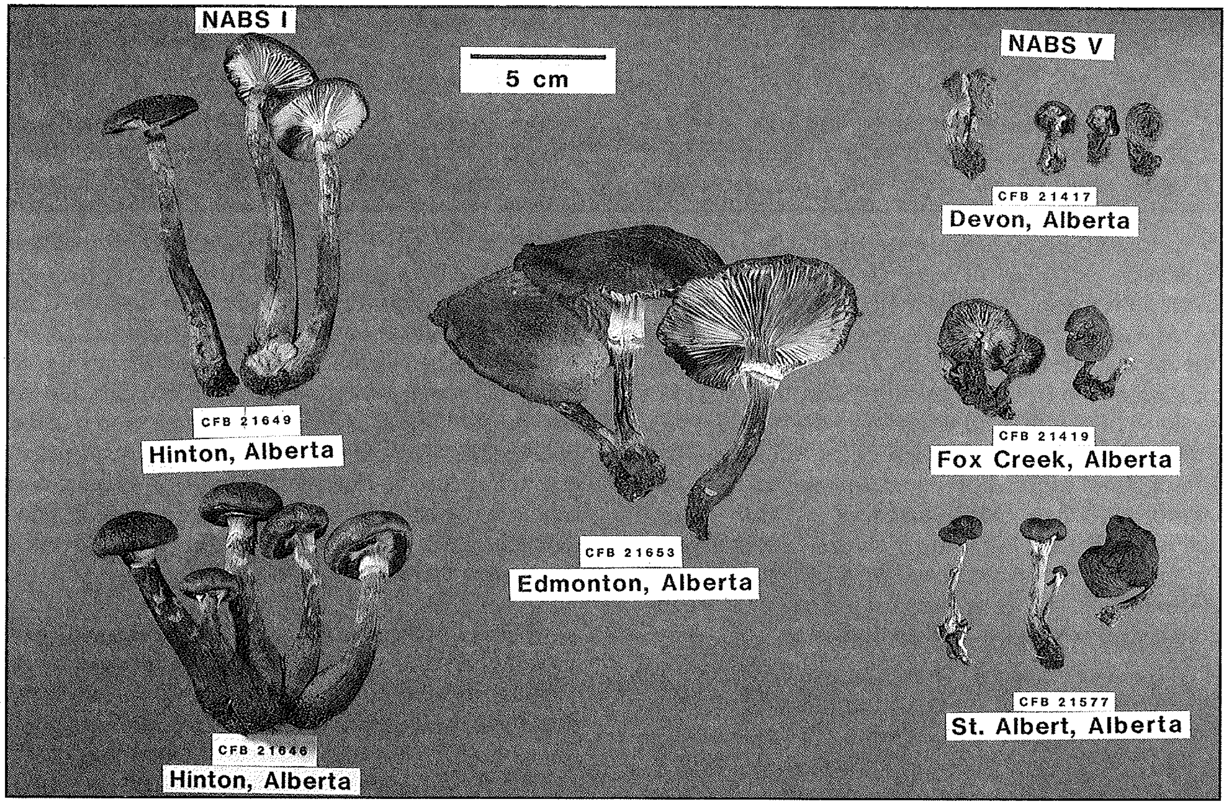


Figure 1. Mushrooms of 2 species of Armillaria found in the prairie provinces. NABS I = *Armillaria ostoyae*; NABS V = *Armillaria sinapina*.

Species of *Armillaria* can be reliably identified by intersterility testing. In general, haploid-single-spore isolates when grown in culture on agar media have a fluffy morphology, whereas diploid isolates cultured from infested wood or from the basidiocarp have a crustose morphology. Single spore isolates from basidiocarps are paired on agar media with single spore isolates from known *Armillaria* species to determine species relationships. If the isolates are interfertile, a crustose colony will form; however, if they are intersterile the colonies remain fluffy. Methodology for this technique is outlined in Wargo and Shaw (1985) and Guillaumin et al. (1991). Other techniques for identifying *Armillaria* species have been described. Korhonen (1978) paired field-collected diploid isolates with known *Armillaria* species haploid-single-spore isolates. If the species were interfertile (same species) then the single spore isolate was converted to a diploid, which can be detected visually. The L-DOPA method of Hopkin et al. (1989) involves pairing an unknown diploid isolate with diploid isolates of known *Armillaria* species on agar media. If the species are not the same a black line develops between the two isolates when incubated in L-DOPA (L-β-3,4-dihydroxyphenylalanine); no line develops between isolates of the same species.

DISTRIBUTION

Armillaria root rot is found from coast to coast in Canada. Several surveys to determine what species are present and their geographic distribution have been conducted across the country. Morrison et al. (1985) found *A. ostoyae, A. sinapina, A. gallica* Marxmüller & Romagnesi, NABS IX, NABS X, and NABS XI in British Columbia. In northern Ontario, Dumas (1988) found *A. ostoyae, A. sinapina, A.*

gallica, and *A. calvescens*. Bérubé and Dessureault (1988, 1989) recorded *A. ostoyae*, *A. gemina* Bérubé & Dessureault, *A. calvescens*, *A. sinapina*, and *A. mellea* in Quebec.

In the prairie provinces, Mallett (1985, 1990) found *A. ostoyae* and *A. sinapina* in Alberta, Saskatchewan, and Manitoba (Fig. 2). *Armillaria calvescens* was found in Saskatchewan and Manitoba. *Armillaria ostoyae* and *A. sinapina* were found in both the boreal and subalpine forest regions. *Armillaria calvescens* has been found, to date, only in the boreal forest. *Armillaria ostoyae* was found from 49°N to 60°N and *A. sinapina* from 52°01′N to 57°27′N. *Armillaria calvescens* was found so infrequently that its range is uncertain. Armillaria root rot occurs in the Northwest Territories and it has been identified on white spruce (*Picea glauca* [Moench] Voss) at Pine Point on Great Slave Lake (Baranyay 1968), but the identity of the species is currently unknown.

In Mallett's (1990) survey, A. ostoyae was the most common species collected in the prairie provinces, comprising 86.3% of all collections. *Armillaria sinapina* was second most common, comprising 12.4% of collections, and *A. calvescens* was the least common species with only 1.3% of all collections. *Armillaria ostoyae* is the species that is found most commonly in all Canadian provinces surveyed (Fig. 3). The species composition of *Armillaria* in the prairie provinces is most similar to that of northern Ontario. This may be related to the preponderance of the boreal forest region in both the prairie provinces and Ontario. Differences in the species composition found in other parts of Canada is probably related to the distinct forest regions.

SYMPTOMS AND SIGNS

Symptoms of Armillaria root rot vary with host species and age of the tree, but generally there can be foliar discoloration, stunting of growth, stress crop of cones (in conifers), resinosis (Fig. 4) or gummosis of the lower stem, and root rot, butt rot or both. There may be noticeably less foliage on affected trees and those that remain are often chlorotic. Pine tree foliage usually turns a dull green, then yellow, before turning red and is retained for approximately one year after death (Fig. 5). Spruce tree foliage turns a dull green but rarely yellows or turns red before the needles drop off. Needle loss can occur quickly in spruce, within weeks of the tree's death. The presence of a white mycelial fan (fungal tissue) beneath the bark in the root collar (Fig. 6) and the brown–black rhizomorphs (shoestring-like structures) growing on the roots or in the soil nearby (Fig. 7) are diagnostic signs of the disease. Foliar symptoms of Armillaria root rot in pine species are similar to those caused by root collar weevil (*Hylobius warreni* Wood and *H. radicis* Buchanan) and winter desiccation damage. Trees suspected of having Armillaria root rot should be examined for evidence of the white mycelial fan beneath the bark in the root collar area and on structural roots.

Basidiocarps of the fungus are often found at the base of dead or dying trees and stumps in late August or early September (Fig. 8). The *Armillaria* mushroom has an annulus (ring around the upper portion of the stem), and a honey colored cap with white gills (Fig. 9). Basidiocarp production in the prairie provinces is often inconsistent; the environmental conditions necessary for their production are not well understood.

Trees with Armillaria root rot may die quickly (within several months of being infected) in the case of young trees, or they may die over a period of several years in the case of older trees. Many mature trees are chronically infected with the disease and may have only a yellow-stringy rot in the butt or roots (Fig. 10). Armillaria root rot is responsible for the Type B category of rot of aspen described by Hiratsuka et al. (1990) (Fig. 11).

Dead and dying trees can be found in disease centers or may be scattered throughout the stand (Fig. 12). Disease centers are openings in the stand where many trees have been killed in a group. Dying trees are often found around the periphery of the disease center. Trees with root rot are prone to windthrow. Disease centers in mature stands can be identified by noting the orientation of the fallen trees to one another. Fallen trees in disease centers will lay crisscrossed, whereas those that result from blow down lay parallel to each other (Figs. 13, 14).

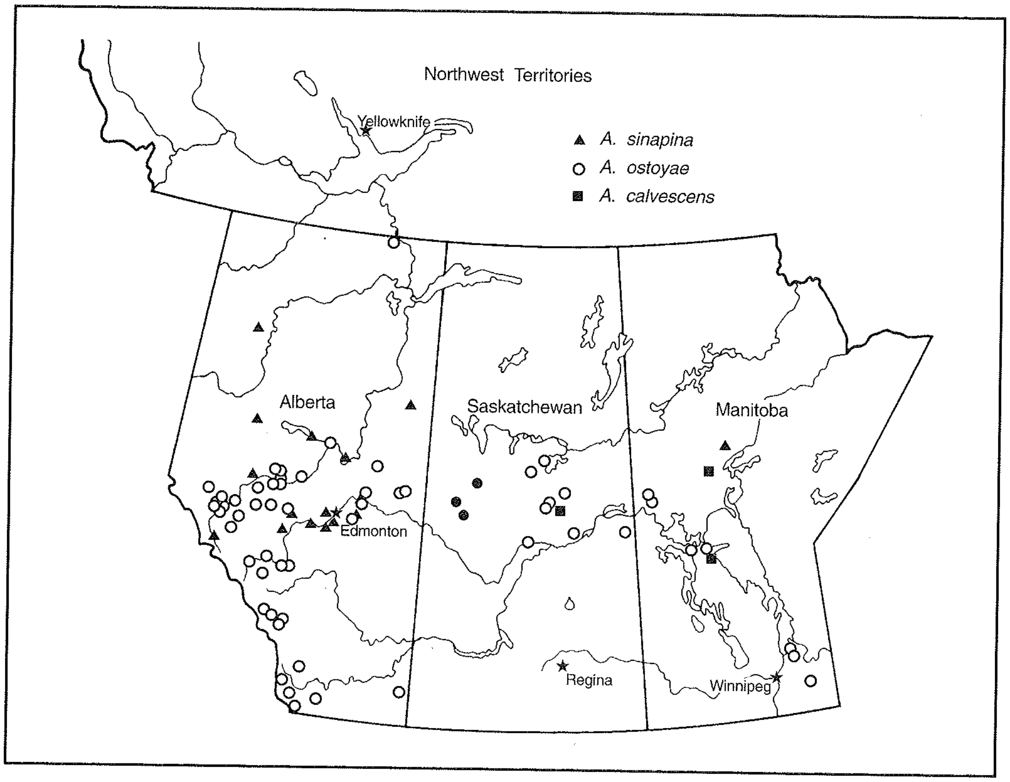


Figure 2. Distribution map of *Armillaria* species in the prairie provinces of Canada.

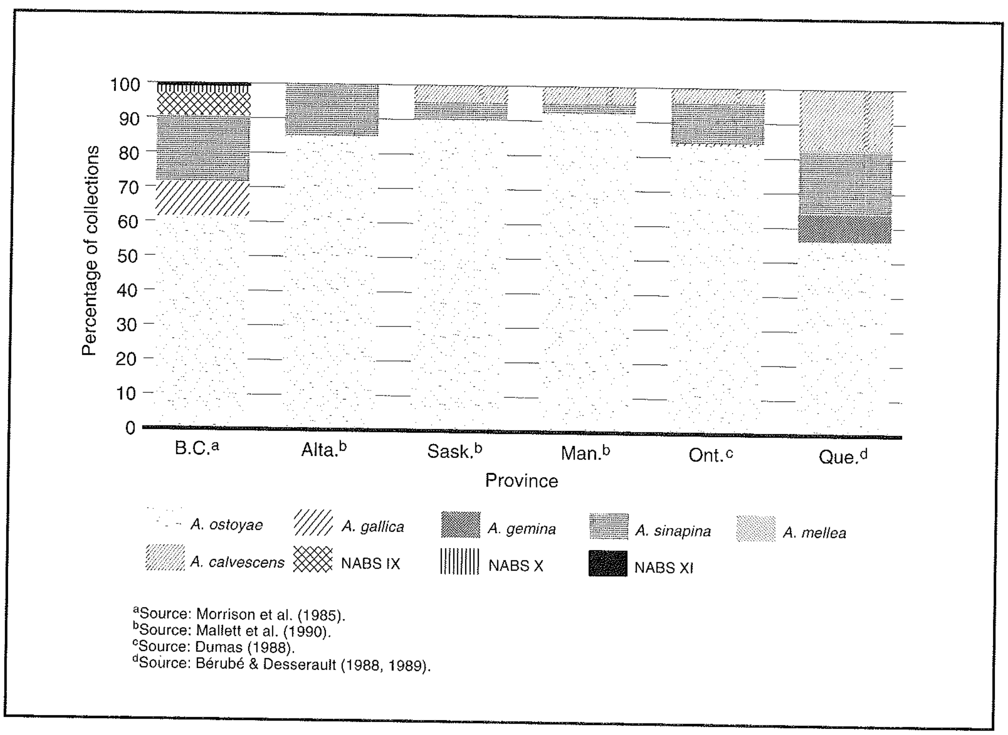


Figure 3. *Armillaria* species found in some Canadian provinces and their relative frequency in collections.

Figure 4. **Resinosis caused by Armillaria root rot.**

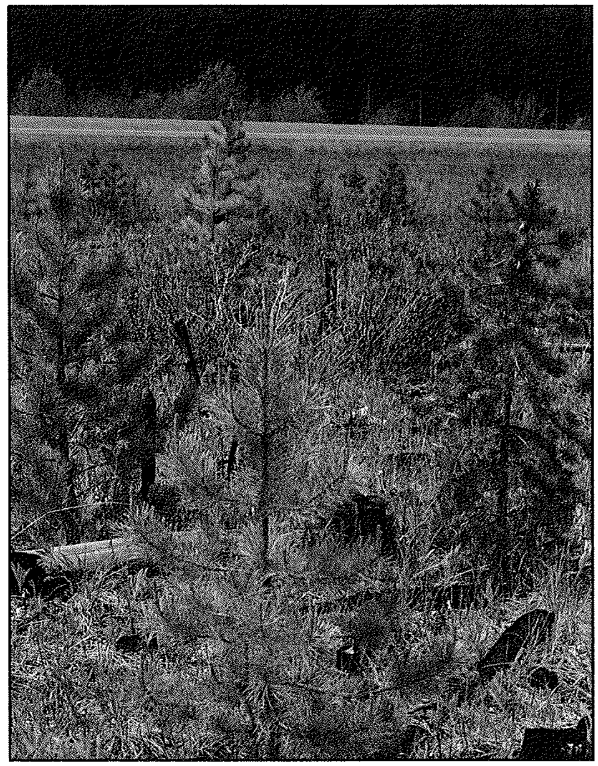


Figure 5. **Foliar symptoms of Armillaria root rot yellowing and reddening of needles.**

Figure 6. **Mycelial fan of an *Armillaria* species.** (Photo courtesy of Mike Grandmaison.)

Figure 7. **Rhizomorphs of *Armillaria ostoyae*.**

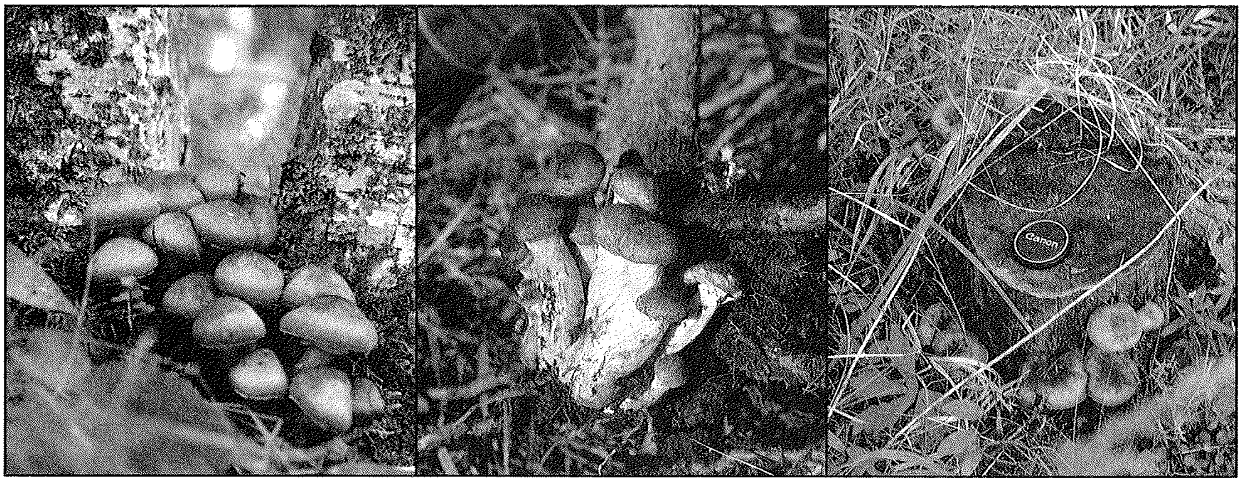


Figure 8. Mushrooms of *Armillaria* species on a stump. (Center photo courtesy of Yasu Hiratsuka.)

Figure 9. A mushroom of *Armillaria ostoyae* with white gills and annulus.

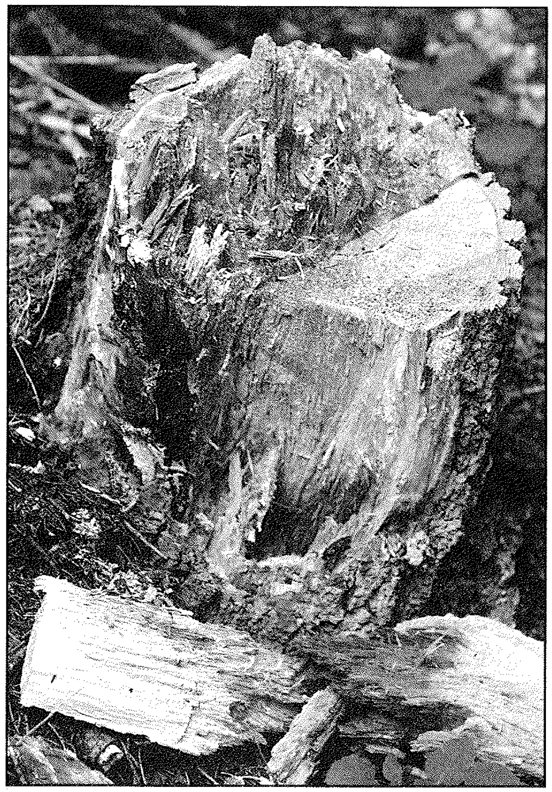


Figure 10. Typical yellow stringy rot of aspen.

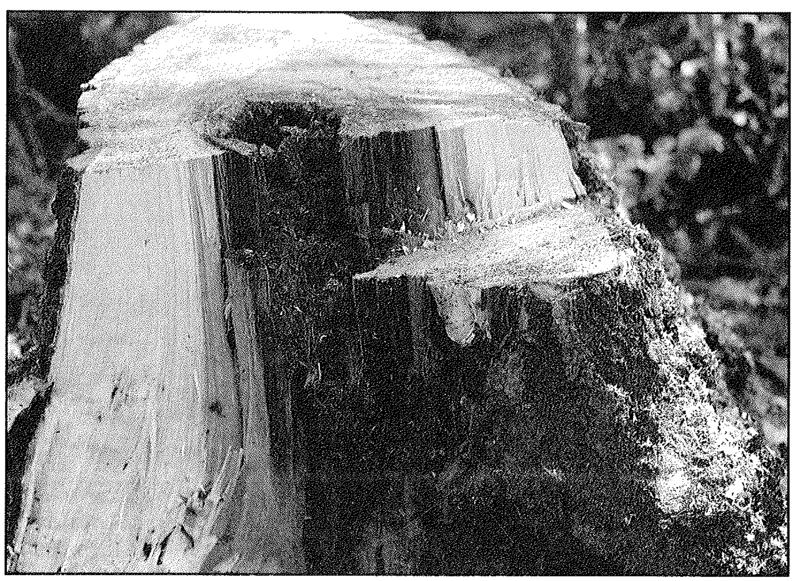


Figure 11. Type B decay of aspen caused by *Armillaria* species. (Photo courtesy of Yasu Hiratsuka.)

Figure 12. An Armillaria root rot disease center.

Figure 13. Blowdown of trees following a windstorm.

Figure 14. Fallen trees in disease centers typically lay crisscrossed.

improved and did not justify the additional time and effort that was taken. Lachance (1979) found that by using aboveground indicators alone, butt rot of white spruce could be successfully predicted 63.5% of the time. If increment cores of the butt were taken, butt rot was correctly predicted 87% of the time.

The Armillaria root rot fungus may be detected in forest soils by the "trap-log" technique (Mallett and Hiratsuka 1985, Mallett 1991). Freshly cut aspen stakes are placed in the soil in the suspected area for 4–6 months (Fig. 15). The stakes are then examined for evidence of colonization by *Armillaria* (Figs. 16, 17). The method can be used for detection of the Armillaria root rot fungus in soil and for determining the extent of spread of the fungus around disease centers. Ip (1991) developed a modified trap-log he called a trap-bag. Conifer bark was placed into nylon mesh sacks and buried in the ground. In comparative tests, Ip (1991) found that trap-bags were more sensitive than trap-logs in detecting the presence of *Armillaria* species; the fungus was easier to recognize using trap-bags than trap-logs.

FIELD DETECTION AND SURVEY METHODS

Armillaria root rot can be detected by aerial photography and ground surveys. Color infrared and true color aerial photography can aid in the detection of disease centers (Gregg et al. 1978; Williams and Leaphart 1978; Meyers et al. 1983; Wallis and Lee 1984). Large disease centers have been detected photogrammetrically at scales up to 1:15 000. Small disease centers can be detected using photographs with scales between 1:2000 and 1:6000. Ground survey methods for detecting and estimating losses in stands have been developed (Jacobi et al. 1981; Bloomberg 1983). These surveys allow detection of the disease, determine incidence, and estimate damage. Root rot surveys based on aboveground symptoms and signs can provide some measure of the incidence of the disease (Lachance 1979; Wallis and Bloomberg 1981); however, the most reliable estimation of root and butt rots comes from aboveground symptoms and signs and examining the roots and root collars, either by increment cores or inspecting the roots and butts of the trees. Wallis and Bloomberg (1981) found that aboveground indicators of laminated root rot alone provided a reliable estimate of the total number of diseased trees and stand area affected. By including internal defects additional trees were identified; however, the reliability of the estimate was not

DAMAGE

Damage caused by Armillaria root rot may be direct such as mortality, creating areas of understocking and growth loss. The disease can also have indirect affects on forests such as increasing the tree's susceptibility to windthrow and other pests. In parks or recreation areas, diseased trees may become hazards to people, vehicles, and structures.

Impact of Armillaria root rot on forest trees in Canada has not been documented well and varies from region to region. For example, Morrison (1981) reported that mortality in British Columbia's coastal forests could be between 2 and 3%, but was usually below 1%; however, mortality in 10 stands from the southern interior forests ranged from 3.6

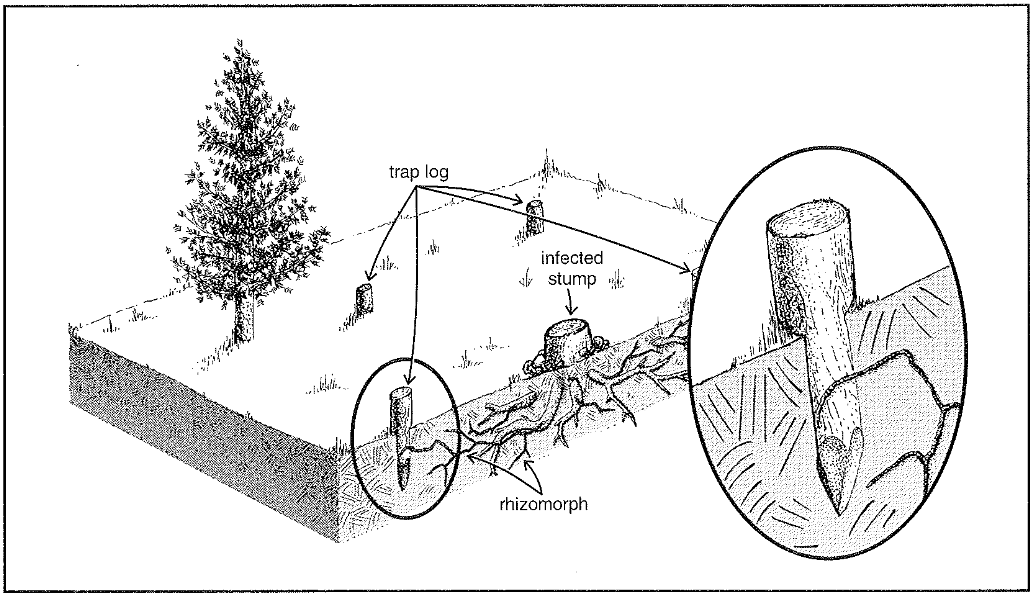


Figure 15. Rhizomorphs from an Armillaria-infested stump attempting to colonize a trap log.

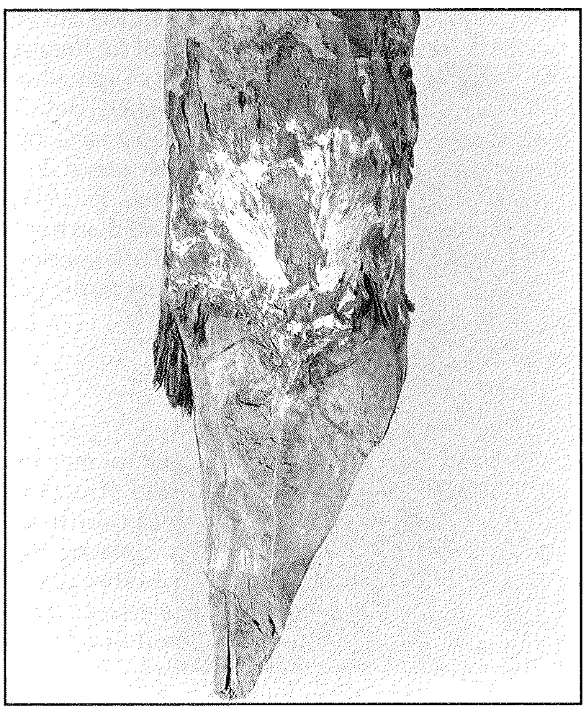


Figure 16. Trap log with bark removed to show white fan of mycelium. (Reproduced with permission from the National Research Council [Mallett and Hiratsuka 1985].)

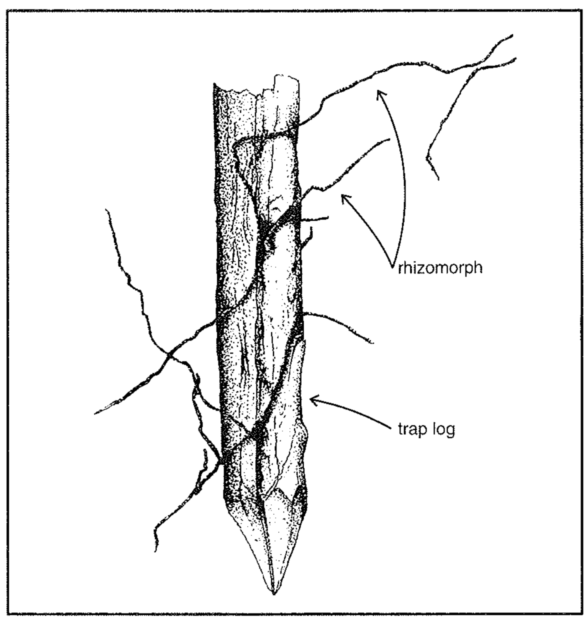


Figure 17. Rhizomorphs growing from an infested trap log.

to 30%, with an average of 14%. Surveys for Armillaria root rot in young stands have been conducted at various times at different locations across Canada and indicate that the disease is of great importance.

Damage to Young Trees

Armillaria root rot is prevalent in young conifer stands and usually causes mortality in trees between the ages of 5 and 25. Several studies have documented losses in young conifer stands in the prairie provinces with mortality ranging from 0 to 25%. In one study, done near Robb, Alberta, the average mortality from Armillaria root rot in naturally seeded young lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) was 13.7 and 15%, 17 and 20 years after the stand originated (Baranyay and Stevenson 1964). Many of the reports are from surveys done in a single year and do not record the accumulated mortality over several years. The disease was identified as the major cause of mortality in thinned 7-year-old lodgepole pine stands in west-central Alberta (Johnstone 1981). More recently, Amirault and Pope (1989) surveyed young lodgepole pine stands throughout west-central Alberta for pest damage and found that Armillaria root rot was one of the primary causes of mortality ranging from 0 to 7.2%. Armillaria root rot has been found to cause mortality in young jack pine (*Pinus banksiana* Lamb.) and white spruce stands in Saskatchewan, although loss figures have not been reported (Riley and Zalasky 1962). The disease has caused mortality in young jack pine stands in northern Manitoba and in black spruce (*Picea mariana* [Mill.] B.S.P.) and white spruce stands in eastern Manitoba. The Manitoba Department of Natural Resources has noted an average accumulated mortality of 25% in young red pine (*Pinus resinosa* Ait.) over 5 years in the southeast region of the province (Westwood 1990). Armillaria root rot is found in the Northwest Territories but no loss figures have been reported.

Elsewhere in Canada surveys have been conducted to determine the damage done by the disease in young conifer stands. Morrison (1981) reported that Armillaria root rot was of particular importance in conifer regeneration in the southern interior forests of British Columbia. In Ontario, Whitney (1988) surveyed plantations of white spruce, black spruce, red pine, and jack pine for Armillaria root rot and found that current annual mortality for all plantations ranged from 0 to 16%. Substantial mortality has been reported in jack pine, red pine, white spruce, and Norway spruce (*Picea abies* [L.] Karst.) regeneration in Quebec (Martineau and Lavallee 1973, 1976). In the Maritime provinces, Magasi (1990) established plots to monitor Armillaria root rot mortality in black spruce and jack pine plantations. He found that mortality in black spruce ranged from 4 to 24%, and in jack pine from 2 to 8%. Armillaria root rot has been described as one of Newfoundland's most serious forest tree diseases (Warren and Singh 1970). Some coniferous plantations in Newfoundland have had mortality as high as 32% due to this disease (Singh 1975).

It is apparent that Armillaria root rot can cause considerable damage to young conifer stands, but the damage is variable depending on many factors that are not understood. Growth losses and incidence of trees infected, but without visual symptoms, are unknown.

Damage to Older Trees

In older trees Armillaria root rot can cause a butt and root rot that can lead to mortality, growth loss, and windthrow. There are reports of pole-sized and mature lodgepole pine and white spruce killed in significant numbers in Alberta (Baranyay 1964; Baranyay and Stevenson 1966; Tripp and Blauel 1969; Ives et al. 1971). Whitney (1988), over a ten-year period, found the accumulated mortality in 43- to 58-year-old white spruce and 43- to 53-year-old red pine plantations to be 7.6 and 11.7%, respectively. Root rot losses from *A. mellea*, *Inonotus tomentosus* (Fr.) Gilbertson, and *Coniophora puteana* (Schum.:Fr.) Karst. in 70- to 111-year-old upland spruce stands in Saskatchewan were determined to be 28% of the total volume (Whitney 1973). Balsam fir (*Abies balsamea* [L.] Mill.) mortality has been reported in the prairie provinces since 1952, and Armillaria root rot has been found associated with many of the dead balsam fir (Thomas 1953; Riley and Hildahl 1964).

In the prairie provinces, Armillaria root rot is commonly found in white spruce and black spruce but has not been implicated as a major source of cull (Denyer and Riley 1953, 1954); however, growth losses and affect on windthrow were not considered. Whitney (1978) found that in 76 sites in northwestern Ontario, *Armillaria* was present in the roots of 42% of the balsam fir, 31% of the black spruce, and 36% of the white spruce examined. He pointed out that in many of the past cull studies, little attention was paid to the root rot fungi. The radial and height increments of balsam fir were substantially reduced in trees with root and butt rot compared to those without rot (Whitney and MacDonald 1985). Bloomberg and Morrison (1989) found that *A. ostoyae* significantly reduced the stem volume growth of Douglas-fir in British Columbia.

In hardwoods, *Armillaria* species are some of the principal decay-causing organisms of trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) in the boreal forest of Alberta (Thomas et al. 1960; Hiratsuka et al. 1990). *Armillaria* species was the most frequently isolated decay fungus from butt infections of trembling aspen and the second most frequently isolated decay fungus from butt infections of balsam poplar; however, the aggregate amount of decay in both poplar species due to *Armillaria* was small. Thomas (1953) found that *Armillaria* species were the main cause of butt rot in poplar at four sample areas in Manitoba and Saskatchewan. Black and Kristapovich (1954) reported that *Armillaria* species were responsible for 0.4% of all cull in aspen poplar sampled in Manitoba and eastern Saskatchewan.

The effect of Armillaria root rot on mortality of hardwood in the prairie provinces is not well known. About 50% of the mature trembling aspen in the campground at Crimson Lake Provincial Park, Alberta, were reported to have been killed or extensively decayed by *Armillaria* (Ives et al. 1973). Basham and Navratil (1975) assessed aspen suckers on cutovers for decay and stain and concluded that Armillaria root rot was one of the most serious threats to the quality of the regenerating stands. This was mainly due to increases in susceptibility to breakage and to mortality. Mortality in young aspen poplar stands has not been studied in the prairie provinces.

HOSTS

Armillaria root rot is a disease that affects a wide variety of plants (Raabe 1962). A list of host species for known *Armillaria* species from the prairie provinces is shown in Table 2. Mallett (1990) found *Armillaria* species associated with sixteen different species of trees and shrubs in the prairie provinces. In addition Klein-Gebbinck (1988) has found *Armillaria* on rose (*Rosa* sp.), common bearberry (*Arctostaphylos uva-ursi* [L.] Spreng.), fireweed (*Epilobium angustifolium* L.), and several graminaceous hosts. *Acer* species, *Larix* species, and the soft pines are also known hosts of *Armillaria* species in the prairie provinces (Hiratsuka 1977).

Armillaria ostoyae caused disease or decay in all of the host species from the prairie provinces that are listed in Table 2 (Mallett 1990). It has been found in all the tree species except willow (*Salix* sp.) and white elm (*Ulmus americana* L.). *Armillaria ostoyae* was the most frequently found *Armillaria* species on conifers in the prairie provinces (95.8% of conifer isolates) and was particularly prevalent in young lodgepole, jack, and red pine stands. *Armillaria ostoyae* was found on 45.4% of the deciduous trees showing Armillaria root rot symptoms and was the species most frequently found on aspen. This species has been associated with both root rot and butt rot of aspen and balsam poplar.

Armillaria sinapina was frequently found on deciduous trees, comprising 52.3% of deciduous trees with Armillaria root rot, but rarely found on conifers, only making up 3.1% of all conifer trees with Armillaria root rot. It had killed the balsam fir, white spruce, jack pine, lodgepole pine, and white elm trees on which it was found and caused a butt rot on aspen and balsam poplar. *Armillaria sinapina* was frequently found on white birch (*Betula papyrifera* Marsh.) and willow (*Salix* sp.), but it could not be determined whether the fungus killed the tree or colonized the trees after they had died.

Armillaria calvescens occurred with about equal frequency on conifers (1.1%) as on deciduous trees (2.3%). Dumas (1988) found *A. calvescens* on dead trees and stumps. Bérubé and Dessureault (1989) and Sabourin et al. (1990) found this species growing on stumps, as well as healthy and declining sugar maple (*Acer saccharum* Marsh.) trees. The importance of *A. calvescens* in causing Armillaria root rot in the prairie provinces is uncertain because it is found infrequently. Figure 18 shows a comparison of *Armillaria* species and frequency on coniferous or hardwood hosts by province. Armillaria root rot was not frequently collected on hardwood trees in Saskatchewan and Manitoba; this probably accounts for the absence of some *Armillaria* species and the relative abundance of others. *Armillaria*

Table 2. Host species for Armillaria root rot in the prairie provinces of Canada (modified from Mallett (1990))

Host species	*Armillaria ostoyae*	*Armillaria sinapina*	*Armillaria calvescens*
Abies balsamea (L.) Mill.	+	+	
Abies lasiocarpa (Hook.) Nutt.	+		
Picea glauca (Moench) Voss	+	+	
Picea mariana (Mill.) B.S.P.	+		
Pinus banksiana Lamb.	+	+	+
Pinus contorta Dougl.	+	+	
Pinus resinosa Ait.	+		
Pseudotsuga menziesii (Mirb.) Franco	+		
Alnus B. Ehrh.	+		
Arctostaphylos uva-ursi (L.) Spreng.[a]	+		
Betula papyrifera Marsh.	+	+	
Epilobium angustifolium L.[a]	+		
Populus L.	+	+	
Populus balsamifera L.	+	+	
Populus tremuloides Michx.	+	+	+
Rosa L.[a]	+		
Salix L.		+	
Sheperdia argentea Nutt.	+		
Sheperdia canadensis (L.) Nutt.	+		
Ulmus americana L.		+	

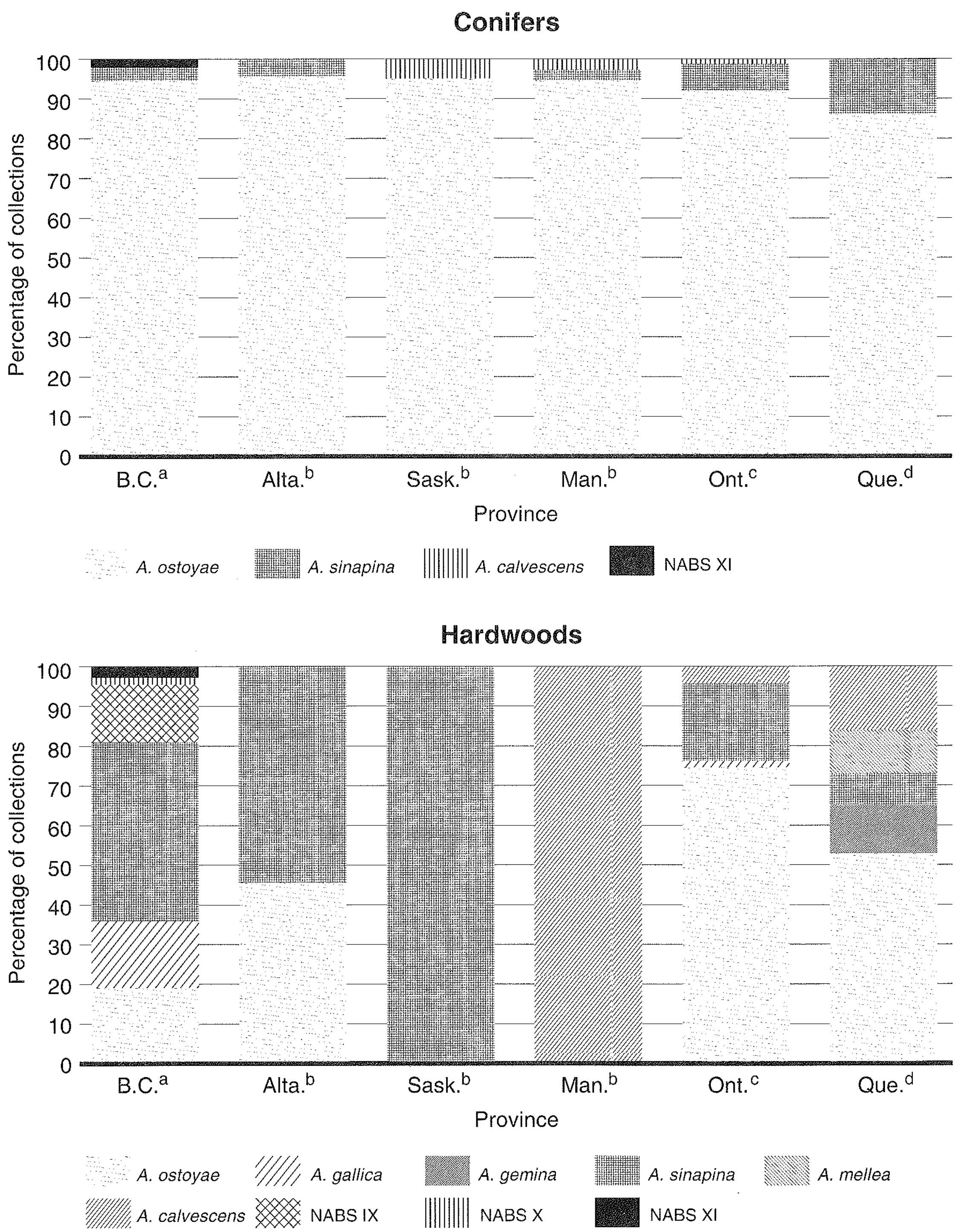
[a] Source: Klein-Gebbinck (1988).

ostoyae is the most frequently found *Armillaria* species on conifers in Canada. This species is also the most frequently collected species on hardwoods in eastern Canada; this is not the case in western Canada.

Armillaria *sinapina* is not commonly found on conifer species in western Canada; it is more common in eastern Canada. Interestingly, *A. sinapina* is common on deciduous trees in western Canada, but it is not common in the east on deciduous trees. *Armillaria calvescens* has not been found west of Saskatchewan and appears to be more common on hardwood species in eastern Canada. These differences may be a reflection of the various forest regions found across the country and/or may reflect variation in different *Armillaria* species populations that cause disease.

Pathogenicity

Few studies have examined pathogenicity (ability to cause disease) of *Armillaria* species to tree species in North America. Mallett and Hiratsuka (1988) inoculated young lodgepole pine seedlings grown in a glasshouse with isolates of *A. ostoyae*, *A. sinapina*, and *A. mellea*. All species of *Armillaria* were pathogenic (caused disease). *Armillaria mellea* was the most pathogenic, infecting 95% of all seedlings with which it was inoculated. It also caused mortality in 83.3% of the infected seedlings. *Armillaria sinapina* was also very pathogenic to lodgepole pine, infecting 76.8% of the seedlings. About 27% of the infected seedlings were killed. *Armillaria ostoyae* was least pathogenic, infecting 33% of the trees; 8% of the infected trees were killed. Mugala et al. 1989 inoculated glasshouse-grown lodgepole pine and white spruce with *A. ostoyae* and *A. sinapina*. *Armillaria sinapina* infected 33.9% of the spruce, 28.7% of the pine, but did not kill any of the trees. *Armillaria ostoyae* infected 54.7% of the spruce, killing 38% of those infected. It infected 28.2% of the lodgepole pine seedlings, killing 19.3% of those infected. The differences in the results of this study and Mallett and Hiratsukas' (1988) study may have been in the



[a]Source: Morrison et al. (1985).
[b]Source: Mallett (1990).
[c]Source: Dumas (1988).
[d]Source: Bérubé & Desserault (1988, 1989).

Figure 18. Armillaria species and their frequency of collection from coniferous and hardwood tree species found in some Canadian provinces.

conditions under which the seedlings were grown. Pathogenicity of the *Armillaria* species in the prairie provinces needs further study to determine the relative susceptibilities of different host species to the *Armillaria* species and the environmental conditions that promote disease.

EPIDEMIOLOGY

Armillaria species inhabit the subterranean portions of trees as well as soil. These decay causing fungi receive their nutrition from woody tissue. *Armillaria* species produce rhizomorphs, (shoestring-like structures) from infested stumps or dead trees. This infested woody material is known as a food base, and it is from food bases that rhizomorphs grow into the soil. The rhizomorphs grow throughout the soil and may attach to healthy roots. Once in contact with a root, the rhizomorphs try to penetrate the root, and if successful, colonize. *Armillaria*-infested pieces of wood may remain active sources of inoculum for decades.

Other means of dispersion are by root-to-root contact with a diseased tree or by contact with infested woody material in the soil. In the coastal forests of British Columbia, the primary means of disseminating this disease in young coastal plantations is likely by rhizomorphs; however, in British Columbia's interior forests the principal means of spread is by root-to-root contact (Morrison 1981). In the subalpine and boreal forests of the prairie provinces rhizomorphs appear to be the primary means of spreading the disease, although infections from root-to-root contact do take place. Klein-Gebbinck et al. (1991) found that rhizomorphs were the primary means of dispersion for the disease in young lodgepole pine stands in west-central Alberta. The role of basidiospores, produced by the mushrooms, in the infection process is not well known, but they are not generally believed to play an important role in the spread of the disease.

In young stands, rhizomorphs grow out from the infested stumps and roots of the previous stand and attack the young, healthy trees, which quickly die. These young dead trees may also serve as a food base for the fungus. Klein-Gebbinck et al. (1991) found that in young lodgepole pine stands in west-central Alberta, most of the rhizomorphs that initiated infections in trees arose from stumps, roots, or woody debris, and that 20% of the infections arose from secondary inoculum, young killed trees. They also found that lodgepole pine trees that were attacked on the tap root or in the root collar region had greater mortality than those that were attacked on a lateral root. Klein-Gebbinck (1988) used nearest-neighbor spatial analysis to determine the spatial relationships between stumps, killed trees, and healthy trees. His findings indicated that there was no relationship between killed trees and stumps or between killed trees and the health of trees that were growing more than 15 cm away. These findings were based on foliar symptoms. Dead trees were examined for resinosis and a mycelial fan but the healthy trees' roots were not examined. It is conceivable that these healthy trees may have had infections on the roots but were symptomless aboveground.

The pattern of mortality from Armillaria root rot can follow three paths: a radially expanding patch of dead trees; dead trees occurring in patches dispersed at random; and small patches of dead trees occurring in young stands, but the patches of mortality fail to expand as the stand ages. The first pattern has been observed in the Pacific Northwest and in Ontario (Shaw and Roth 1976; Morrison 1981; Huntley et al. 1961). The disease centers can become quite large, 0.2–0.3 ha in the southern interior of British Columbia (Morrison 1981). The second pattern of mortality has been found in New Zealand and Australia (Mackenzie and Shaw 1978; Pearce et al. 1986). The third pattern of mortality has been observed by Morrison (1981) in the coastal forests of British Columbia. Small groups of young trees, 5–10 years old are killed but mortality usually does not occur after age 25. Both patchy mortality and radially expanding disease centers occur in the prairie provinces; patchy mortality occurs in the subalpine and boreal forests. Radially expanding disease centers have been observed in red pine plantations and naturally occurring jack pine stands in southeastern Manitoba. The radially expanding type of disease center has also been found in Alberta and Saskatchewan in mixed stands of pine and spruce, but these are thought to have been caused mainly by *I. tomentosus*. The rate of spread of *Armillaria* root rot disease centers has been determined by several researchers. Rishbeth (1968) calculated the rate of spread of a disease center in a Douglas-fir stand as 1.1 m/yr. Shaw and Roth (1976) determined that the average rate of radial growth in a disease center in a ponderosa pine stand was 1 m/yr. The rate of spread is probably dependent upon a number of factors such as *Armillaria* species, site, and host species. No spread rates have been calculated for *Armillaria* root rot centers in the prairie provinces.

FACTORS AFFECTING *ARMILLARIA* ROOT ROT

The status of *Armillaria* species as important pathogens has been a source of considerable controversy. Many reports have cited *Armillaria* as a secondary pathogen that attacks trees that have been stressed in some way. These reports may have been based on the belief that the disease was caused by a single species. It is now known that there are many species of *Armillaria* that can cause root rot and that these species have differing abilities in causing disease. Other factors that may influence the severity of the disease include environment and forest management practices.

Several environmental factors have been suggested as potentially predisposing hosts to infection. Suppressed trees or those exposed to reduced light intensity have been identified as susceptible to infection (Redfern 1978). Other researchers have found that soil nutrients, drought, waterlogging, insect and herbicide defoliation, as well as frost can predispose trees to attack. Other studies have found the fungus to be a primary pathogen capable of killing healthy trees. Shaw and Roth (1978) suggested that damage is probably determined by a combination of factors including host susceptibility, stand structure and composition, environment, fungal strain, and inoculum characteristics.

Entry et al. (1986) investigated the effects of light and nutrients on infection of western white pine (*Pinus monticola* Dougl.). They found that seedlings that had a full light treatment and complete nutrients had less infections than those that received full light and incomplete nutrients and those that received full nutrients but were grown in reduced light. Redfern (1978) found that shade-intolerant species had more infections when inoculated with *Armillaria* and kept under low light conditions than those kept in full light.

Singh (1981) found that in Newfoundland rhizomorph growth and distribution was dependent upon several site and soil characteristics. Rhizomorphs were most abundant in the humus layer (0–15 cm) and least abundant at a depth of 15–30 cm. In England, Morrison (1976) found that in dry soils rhizomorphs were found deeper than the upper 5 cm, whereas on moist soils most of the rhizomorphs were in the upper 5 cm. Shields and Hobbs (1979) identified soil chemical properties that were associated with Armillaria root rot in Douglas-fir and grand fir (*Abies grandis* [Dougl.] Lindl.). Armillaria root rot in Douglas-fir was associated with low soil nitrogen and pH. In grand fir, root rot was associated with low soil calcium and phosphorous but high potassium levels. Singh (1983) examined the effects of combined pH and low soil nutrients on Armillaria root rot on conifer seedlings. He found that there was greater damage by the disease in seedlings grown in soils low in nutrients and having a low pH. Whitney (1984) found that Armillaria root rot was more severe in white spruce, black spruce, and balsam fir grown on course textured sandy soils than fine textured silty soils. He also found that black spruce, white spruce, and balsam fir grown on moist-to-wet sites were less susceptible to the disease than if they were grown on dry sites.

Blenis et al. (1989) tested four different soils from west-central Alberta to see if they influenced Armillaria root rot of lodgepole pine. Their results show that soil type affected inoculum viability, rhizomorph production, infection and death of trees. The soil in which trees had the highest periodic annual increment had the least number of trees infected; however, the soil in which trees had the smallest periodic annual increment did not have the greatest number of trees infected. The soil with the greatest number of infected trees was a sandy loam, whereas the other soils were loams or clay loam. In contrast, W.G.H. Ives (pers. com., October, 1988) observed that in west-central Alberta Armillaria root rot is more damaging on high productivity sites. The reasons for the differences in the observations from these two studies are not clear.

Root rot organisms have been associated with insects in causing tree damage. Armillaria root rot has been associated with several insect pests of conifers, including bark beetles (Cobb et al. 1974; James and Goheen 1981; Hinds et al. 1984), spruce budworm (Sterner 1970; Raske and Sutton 1986), jack pine budworm (Mallett and Volney 1990), and woolly aphids (Hudak and Singh 1970; Hudak and Wells 1974). In the prairie provinces spruce budworm, jack pine budworm, mountain pine beetle, and spruce beetle may all be associated with Armillaria root rot to a certain degree. It is currently unknown whether Armillaria root rot is associated with forest tent caterpillar of aspen.

Forest management practices may have an affect on incidence of Armillaria root rot in regenerating young stands. Initiation of disease centers has been noted to coincide with harvest operations (Wargo and Shaw 1985.) Thinning operations in young stands was found to increase Armillaria root rot in western red cedar (Koenigs 1969) but not in young ponderosa pine (Johnson and Thompson 1975; Filip et al. 1989). In some areas of west-central Alberta incidence of Armillaria root rot in young lodgepole pine stands increased after thinning. Use of herbicides to control unwanted species may increase Armillaria root rot in regenerating stands. Basham (1982) found that the incidence of Armillaria root rot in aspen suckers that had been sprayed with 2,4-dichlorophenoxyacetic acid (2,4-D) but were not killed was greater than in unsprayed suckers. Pronos and Patton (1977a) found that Armillaria root rot was common in red pine growing on sites that had been sprayed with chlorophenoxy acid herbicides to eliminate oak, with a mortality rate of 12–37%. *Armillaria* was found to quickly colonize the herbicide killed oak (Pronos and Patton 1977b), and more rhizomorphs have been found to be produced from trees that were killed by herbicides than those killed by manual girdling (Pronos and Patton 1979). There have been no studies in Canada to determine the interaction of herbicides and Armillaria root rot in conifer regeneration.

CONTROL

Control of Armillaria root rot is largely predicated by the value of the resource. Expensive control measures may be considered in high value seed orchards or genetic improvement plantations but may not be economic in regenerating pulpwood stands. Specific control recommendations for the prairie provinces have yet to be developed because the disease was not well studied in the past. With the new knowledge of the presence of at least three species of *Armillaria*, control recommendations will be developed as the behavior of each of these species becomes known.

Control measures used for Armillaria root rot can be grouped into three major types, silvicultural, biological, and chemical. The last type is impractical for use over a large area and cannot be used in Canada because there are no chemicals currently registered for control of Armillaria root rot.

Silvicultural control measures include avoidance of hazardous sites, site preparation, thinning, and method of establishment of regeneration. There is evidence that some sites may be more hazardous for Armillaria root rot than others. Blenis et al. (1989) have some evidence that certain soil types of west-central Alberta are more conducive to Armillaria root rot than others. Sites that have had a root rot in the previous stand are potentially high risk stands in the regeneration phase. Efforts should be made before harvesting to determine if a stand is diseased and the stand area affected. A decision can then be made as to whether inoculum reducing methods such as stump pulling or root raking should be used during site preparation. These methods are expensive and may not be justified on certain sites. Morrison (1981) has recommended removal of stumps and roots from the disease center and a 20-m-wide strip around disease centers. Large stumps and roots must be removed from the soil for the treatment to be effective. It has been demonstrated in British Columbia's southern interior forests that whole-tree harvesting followed by root raking can reduce mortality in lodgepole pine, Douglas-fir, and other species (Morrison et al. 1988). The debris may be left on the soil surface because it dries out quickly and is unsuitable for the fungus. Morrison (1981) has also recommended that thinning not be done in heavily infected stands (>10 disease centers/ha). In stands with only a few disease centers, trees can be thinned.

Efforts should be made in mixed-wood forests to avoid damaging conifer stems and roots while harvesting aspen. There may be some concern that *Armillaria* in aspen stumps could attack the remaining spruce. Stanosz and Patton (1987) found that Armillaria root rot may have an affect on number and length of aspen poplar rotations. The disease increased significantly in aspen suckers when the rotation was shortened.

Methods of regenerating forests may also have an affect on the disease. Singh and Richardson (1973) present evidence that, in Newfoundland, bare-root stock of various spruce species were very susceptible to Armillaria root disease compared to containerized stock and seeded areas.

Morrison (1981) has identified various species and their relative susceptibility to Armillaria root rot. *Abies* species are considered to be most susceptible whereas lodgepole pine, spruce species, and hardwoods were considered to be moderately susceptible. In the prairie provinces relative susceptibility of tree species to the disease are now being investigated. Factors such as site and which *Armillaria* species are present should be considered. Various species of fungi are antagonistic to *Armillaria*. Dumas (1992) has isolated several species of bacteria including *Pseudomonas fluorescens*, *Pseudomonas* sp., *Enterobacter* sp., *Bacillus* sp., and *Agrobacterium radiobacter* that inhibited growth of *A. ostoyae* in culture. No fungi or bacteria are currently being used to control the disease in Canada.

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